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# *THE ENTERON OF THE CAYUGA LAKE LAMPREY.*[*]

*Prize Paper in Animal Histology.*

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## INTRODUCTION.

The interest of zoologists has long been attracted to that group of the vertebrate branch to which the lampreys belong. Standing isolated from all other classes, represented by so few genera and species, and these forms exhibiting both generalized and highly specialized characters, the Marsipobranchs have offered an attractive field for investigation. As early as 1826 an extensive memoir was published by Rathke (47) on the structure of the brook lamprey, followed a year later by a similar study of the larva. Between the years 1834 and 1843 Johannes Müller's (40) series of articles on the comparative anatomy of the myxinoids appeared, in which the general features of the two groups of marsipobranchs are compared. The epoch marking contribution on this subject is due, however, to August Müller (39), who in 1856 discovered the true relations between the larva, previously known as *Ammocœtes branchialis*, and *Petromyzon Planeri*, from which point dates the more comprehensive study of these forms. Since that time embryologists, comparative anatomists and systematists have added to knowledge concerning these interesting animals.

The purpose of this investigation has been to work out as completely as time permitted the enteric structure of the Cayuga

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Lake Lamprey (*Petromyzon dorsatus, Wilder**). As far as ascertained no work has been done on *Petromyzon marinus* excepting in gross anatomy and physiology, while both the histology and gross anatomy of *Petromyzon planeri* have been extensively studied.

With the exception of the contribution by Gage (15) in which he considers some of the features showing the changes undergone during the life history of the lake and brook forms, no special investigations have been made on the structure and metamorphosis of the marine, lake and brook lampreys found in America.

I wish to express my appreciation for the abundant material and facilities placed at my disposal by the Anatomical Department of Cornell University, and for the wise direction and helpful suggestions given by Professor Gage personally throughout this investigation.

## MATERIAL AND METHODS.

The adult form used in this investigation is the Cayuga lake lamprey (Fig. 1). By some writers it is considered a distinct species, while others think it is a land-locked form of *Petromyzon marinus*. If the first supposition is true it is *Petromyzon dorsatus, Wilder*; if the latter, though there is a very close resemblance almost identity between this lake lamprey and *Petromyzon marinus*, the great difference in size and its life in fresh water indicate a species in course of formation. The larvae (Fig. 2), were obtained from a breeding place used by both the lake and brook lamprey, so that until transformation was fairly well advanced it was impossible to say whether they were the young of the brook or of the lake form. Specimens of both larvae and adults were obtained during the months of October to May, adults were also obtained in June and young larvae in July and August, giving the conditions for the adults during eight months and for the larvae during ten months. Some were used as soon as brought in and others were kept for a considerable time in running water thus giving the two conditions of fasting and digestion. The adults varied in size from 29 to 38 centimeters in length and the larvae from 2.5 to 16.5 centimeters. The larvae studied were caught from July to May; the very young ones in July and those during transformation from August to December.

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*By Jordan (29) and Meek (37) the lake lamprey from the lakes of central New York is considered a small form of Petromyzon marinus, but Gage (15) after a consideration of all the evidence thinks it a distinct species.

The following hardening materials were used in the preparation of specimens for histological work; (1) Erlicki's fluid (Potassium bichromate, 2 parts: copper sulphate 1 part; water 100 parts). Tissue was put in this mixture for 5–6 days then washed well for an hour or more in water and put for one day each in 50, 67, and 82 per cent. alcohols. (2) Mercuric chloride was added to normal salt solution until the mixture was saturate. Tissue was hardened in this from 3 to 4 hours, washed thoroughly in 67 per cent. alcohol for a day, changing the liquid several times, and then put into 82 per cent. alcohol. (3) Flemming's fluid (1 per cent. chromic acid, 15 parts; 2 per cent. osmic acid, 4 parts; glacial acetic acid, 1 part). Tissue was left in this for twelve hours, washed well in water and put into 50, 67 and 82 per cent. alcohols for one day in each. (4) Gage's picric alcohol (17) (95 per cent. alcohol, 250 cc. water, 250 cc. picric acid crystals, 1 gram). Tissue was put into this hardener for 12–48 hours the liquid being changed once or more during the time. It was then put into 67 and 82 per cent. alcohols for 1 day each. (5) Picro-aceto-sublimate, (50 per cent. alcohol, 1,000 cc.; glacial acetic acid, 5 cc.; mercuric chloride, 5 grams; picric acid, 1 gram). Tissue was treated the same as with mercuric chloride excepting that 50 per cent. alcohol was used first instead of 67 per cent.

Imbedding was done in both paraffine and collodion. For the former method tissue was dehydrated 12–24 hours in 95 per cent. alcohol, put in chemically pure chloroform for a day and then into chloroform paraffine (4 parts paraffine, 1 part chloroform) and kept in a warm place to infiltrate for four to five days. At the end of this time it was imbedded in pure paraffine. Sections were arranged serially on the slide, coated thinly with Mayer's albumen and slightly heated, the paraffine being removed by xylol. Finding this method of securing the sections to the slide unreliable the following plan was adopted: Sections were treated as described above but instead of heating them a wash of ¾ per cent. collodion was spread over the whole surface and allowed to dry before putting the slides into xylol. This was found perfectly effectual in fastening on the sections and by it all necessity of heating was avoided. Benzene was tried instead of xylol and proved equally good ; as it was found advantageous to have the liquid for removing the paraffine as free as possible from dissolved paraffin, benzene was used exclusively and frequently renewed.

For collodion imbedding, tissue was treated according to Fish's Castor-thyme oil method (14) as follows : Dehydrated in 95 per cent. alcohol for 12–24 hours, put in ether-alcohol (equal parts of each for 12 hours, 2 per cent. collodion for 24 hours, 6 per cent. collodion 24 hours in which it was finally imbedded. After hardening in chloroform for an hour or more it was put into a mixture of three parts thyme oil to one part castor oil. This rendered the collodion clear and tough and the tissue was then cut in the same mixture. The sections were arranged on the microtome knife and by laying tissue or other thin paper upon them and carefully drawing to the edge of the knife they could be transferred to the slide without disarranging them, to which they were fastened by a few drops of ether-alcohol after the removal of all the oil possible. The slides were left in 95 per cent. alcohol for 6–24 hours to remove the remaining oil.

Different stains were used. The most satisfactory were Gage's aqueous hematoxylin, hydrochloric acid carmine, picro-fuchsin-hematoxylin, Delafield's hematoxylin, and picric alcohol. The aqueous hematoxylin (18) gave very good results with picric alcohol as a counter stain but did not take effect if the tissue had been treated with chromic acid, even if it had only been used in a ¼ per cent. solution to kill the animal. In the latter case Delafield's hematoxylin was satisfactory. The time of staining varied with the hardener. After picric alcohol the stains act quickly but after Flemming's fluid more slowly. For the study of cell contents tissue was treated with one per cent. osmic acid and cut in gum arabic on the freezing microtome.

Serial sectioning was employed almost exclusively. Some isolation preparations were made in 35 per cent. caustic potash, $\frac{1}{10}$ per cent. osmic acid, and ¾ per cent. Müller's fluid, for the study of individual cells. With the exception of these and the osmic acid preparations, all sections were mounted in Canada balsam ; the others were prepared in glycerine jelly, equal parts of glycerine and water, Farrant's gum glycerine medium, or potassium acetate. All the hardeners gave good results. Flemming's fluid was the best in some respects while picric alcohol contracted tissue as little as any. Fish's picro-aceto-sublimate also gave clear results.

### GENERAL RELATIONS OF THE ENTERON.

*Larva.*—The general relations of the larval enteron are very simple. There are to be recognized three parts, a branchio-pharyngeal chamber, a middle part consisting of a small tube and a third division, the intestine. The first is a large cavity into which the mouth and seven pairs of lateral branchiopores open, water flowing into it constantly from the mouth and out through the pores. Arising from its caudal end first as a groove on its ventral surface and later closing up as a complete tube is the second part of the enteron. It is small in diameter and suggestive in its shape of an esophagus, but is all there is to represent both that part and the stomach. It is short, not more than two centimeters long in the full grown larva. The third division is undoubtedly the intestine, though it begins with a dilation that, following the narrow tube, seems to be fitly called the stomach; but the entrance of the bile duct at the cephalic end of this part shows, as in higher forms, the beginning of the intestine. The enlargement mentioned above projects slightly cephalad of the entrance of the esophageal-stomach so that in cross section it appears surrounding the smaller tube. The intestine continues caudad, tapering gradually to the end. A fold of mucosa, the *typhlosole*, projects into the lumen, beginning dorsally in the sudden dilation and continuing till about one or one-half centimeter from the vent, ending ventrally thus completing one half a spiral turn. The whole canal from the end of the branchial cavity lies free in the coelum, unconnected by a mesentery; the only union is toward the caudal end of the body where there are dorsally a few fine thread like bands, perhaps vascular in nature; also, close to the vent, slight dorsal and ventral mesenteries are found.

The liver is situated ventrad of the esophageal-stomach, if so this part may be called, and connected with the alimentary canal by the bile duct, coeliac artery and portal vein alone. The gall bladder is buried in the tissue at the right side in the cephalic end and is a distinct feature in fresh specimens, being evident as a green, comparatively large-sized area. The duct leaves the liver dorsally about the middle of its length and side by side with the coeliac artery enters the cephalic end of the intestine. The enlargement showing the beginning of the intestine, the entrance of the bile duct and the beginning of the typhlosole are all at nearly the same level, the whole transition being made in about one millimeter. The artery enters the typhlosole and continues throughout its length giving off numerous branches to the intestinal wall. The portal vein arises at the caudal end of the intestine and on the dorsal side opposite the intestinal fold. At first it lies just under the ectal layer of the intestinal wall, but about the middle of its length it becomes free and is then known as the subintestinal vein (Fig. 7.) At intervals there are small veins uniting it with the intestine and just caudad of the point of the liver a large vessel joins it. The portal vein enters the caudal point of the liver and lies along its dorsal surface just within the tissue till near the middle of that organ where it enters more deeply, breaks up into capillaries which reunite to form the hepatic vein, the latter flowing into the sinus venosus from the ventro-cephalic part of the liver.

*Adult.*—The enteron of the adult lamprey may also be recognized as divided into three parts, the pharynx, esophagus and intestine. In the adult the continuity of the respiratory and digestive systems found in the larva is lost, excepting for this pharynx from which both bronchus and esophagus arise.

The esophagus is a small tube lying on the dorsal wall of the low, much restricted bronchus and opening from the pharynx by a small orifice just dorsad of the tongue. The esophagus swerves to the left, passes by the pericardial cavity and leads directly into the intestine by an orifice having valve-like lips. The intestine is much expanded and projects cephalad into a little blind pocket; between the opposed walls of this and the esophagus is imbedded a small gland-like structure.

The much enlarged intestine tapers gradually, showing a number of spiral turns; at about two thirds of its length a strange reversal of the direction of the turns takes place (Fig. 3.) The number of complete turns varies from four to six, and the grouping cephalad and caudad of the change also varies as does the position of the point of change, the latter being either dorsal, lateral or ventral.

It seems as if the intestine might have been grasped at this point and rolled over giving a right-handed spiral to the anterior part and a left-handed to the posterior. But this would result in an equal number of turns in the two directions which is not the case. The most frequent number of twists is five and these are usually arranged two caudad and three cephalad of the change; this gives a complete turn more on one side than on the other. This difference may perhaps be produced by more rapid growth at the cephalic end. Whatever the explanation, this twisting is evidently a contrivance to accommodate the increased length of the intestine which even with this arrangement is always longer than the abdominal cavity. A *spiral valve* or *typhlosole* traverses the intestine, starting from its cephalic end and following the spirals to terminate ventrad not far from the vent. The relations of the intestinal turns and this valve show conclusively that the twists are produced by a spiral coiling of the whole canal. In this respect this spiral valve differs in structure from those of any of the other vertebrates possessing such a modification. Many forms of intestinal valves are found among elasmobranchs, ganoids, and dipnoans and in all cases are composed of spiral folds of mucosa inside muscular walls which show no evidence of twisting.

For this reason it is hard to see how the condition in the lamprey can be in any way generalized though Balfour (2) says that the spiral valve of the elasmobranchs arises as an entally projecting fold. Even the simplest adult forms among the rays described by Parker (45) give no suggestion of the condition shown in *Petromyzon*. The larval fold closely resembles the typhlosole as seen among invertebrates, but this resemblance is lost in the adult.

The intestine is entirely free from the body wall throughout the greater part of its length. Near the caudal end some dorsal bands are found much larger in proportion than those of the larva and varying in number from three to six (Fig. 4.) These are undoubtedly vascular in nature some being veins and others both veins and arteries (Fig. 5), varying in size from mere threads to a large group of vessels. Near the vent short ventral and dorsal mesenteries are present.

The typhlosole is traversed throughout its length by two large vessels, the intestinal artery and vein (Fig. 9,) the former is a branch of the coeliac which divides into two, one part going to the liver and one entering the typhlosole. At the caudal end of the intestine there are two to three arterial branches from the aorta, the largest together with the one or two veins forming the largest dorsal band (Fig. 5). This artery enters the typhlosole at its caudal end and anastomoses without apparent reduction in size with the descending mesenteric artery. It may thus be called the inferior mesenteric artery. The other branches from the aorta may run out into capillaries on the intestinal wall or as in a specimen of *Petromyzon marinus*, the one next caudad to the inferior mesenteric may unite with it just before entering the fold.

Following the portal vein back from the liver it is found to decrease in size for a certain part of its length and then remain the same. Almost at the level of the large vascular band it suddenly comes to the ventral surface of the intestine and going dorsad on either the right or left side forms, together with the inferior mesenteric artery, the above mentioned large dorsal band. It is sometimes divided into two by the artery and sometimes not (Fig. 5.) Tracing the vessel up it is found to connect with a large sinus situated between the cardinal veins. This sinus extends from near the caudal end of the canal to the pericardium where it ends blindly. It is very thin-walled and contains many fibrous septa that appear to divide it more or less completely into two at the cephalic end. Sometimes it is found full of blood and sometimes not. Besides the connection with the intestinal vein there are many openings into the cardinals at irregular intervals and all the blood of the gonads and kidneys is poured into it. Fine injections were made from different parts of the sinus cephalad and caudad and also through the portal vein. The result showed that the flow of liquid is more ready caudad and any such injection does not fill the cardinals posterior to the mesenteric vein, the flow apparently being concentrated into the intestinal vein. There is no cephalic connection between the sinus and the cardinals or auricle, the sinus terminating blindly. That this is a blood vessel is beyond question ; that it has no communication with the circumsesophageal blood sinuses described by Ewart (12) excepting through the medium of the heart is evident and the suggestions as to the caudal flow of blood are confirmed by some observations of the French physiologist, Bert, (5) on *Petromyzon marinus.* He says as follows: "l'animal étant immobilisé par curare, comme il va être dit, je l'ouvre sur le flanc; les grands sinus sous cardinaux sont flasques; graduellement ils se remplissent de sang; ce sang vient du côté du cœur. Une ligature, placée sur la veine qui fait communiquer le système rénal avec le système hépatique (arc hépato-néphrétique de Gratiolet), montre que le sang (l'expérience dure environ une heure) va du rein au foie."

This sinus is then evidently a means of introducing into the portal system a large amount of venous blood that comes from urogenital and body veins. This makes the lampreys possessors of a connection between the genital and portal veins and gives them one more feature in common with the very dissimilar members of their class, the myxinoids. The descriptions given of the latter by Johannes Müller (40) represent them to be alone among marsipobranchs in the possession of this feature.

The liver is placed ventrad of the intestine firmly attached to it and to the pericardium by connective tissue. It is a bright yellow color during most of the animal's life, becoming green at the spawning season. There is no gall bladder and no duct and the external portal vein of the larva is entirely gone.

These observations agree in general with those recorded on *Petromyzon Planeri* and *Petromyzon marinus.* Schneider (50) speaks of four, fine bands at the caudal end of the larval intestine of *Petromyzon Planeri* and calls them veins. He also says there is an hepatic branch of the coeliac artery which Chas. Julien (30) fails to find and thinks himself justified in saying that it does not exist. A branch corresponding to this one of Schneider's has not been found in the larvae studied. No description could be found of a condition similar to that of the adult portal vein in any of the writings consulted, but from Bert's (5) work on *Petromyzon marinus* it has evidently been recognized in that form. All references to the intestinal turns in *Petromyzon Planeri* give three and one half to four as a maximum number and their development during metamorphosis is mentioned by Nestler (41). The dorsal sinus has been described in *Petromyzon Planeri* by Rathke (47), Müller (40), Langerhans (35), Schneider

(50), but with the exception of the last writer, all were inclined to call it a lymph space as also has Parker (44), in *Petromyzon marinus*. Schneider (50) calls it a blood space and even a vein and says that blood flows from it to the cardinals and so to the auricle. He considers the numerous venous sinuses of the lamprey indicative of degeneration, a view pointed out first by Dumeril (9).

## HISTOLOGY OF THE LARVAL ENTERON.

The larval enteron shows the presence of both muscular and mucosal tissues (Figs. 6, 7,) though in a somewhat modified form and exhibiting rather unusual features. The musculature is composed of an ectal longitudinal and an ental circular layer (Fig. 14.), which are easily distinguished in isolation preparations. The muscle cells (Fig. 14 A.) are small, fusiform and very variable in size ; they are massed into strands by the overlapping of the fusiform ends and the strands lie parallel to each other with small interspaces. The two layers are placed at approximately right angles with each other. As peristaltic movements had never been seen the intestine of a larva thirteen centimeters in length was tested by stimulation with electricity. A dry cell battery with an interrupted current was used, but failed to produce the slightest movement even on the application of its full power. The efficiency of the current was shown by the rapid contraction of the body muscles when stimulated. Parts of the intestine were put on a slide and watched under the microscope during stimulation but even this failed to reveal contraction. There was nothing unusual in the appearance of the muscle cells, They resembled ordinary unstriated muscular tissue.

The layer intervening between the musculature and the epithelium (Figs. 6, 7, 12,) resembles cavernous tissue. The vessels are small at the caudal end of the canal increasing in size on going cephalad where they are evidently filled with blood corpuscles thus indicating beyond a doubt their vascular nature. This cavernous condition is especially emphasized in young larvae of from two to three centimeters in length. In these the vessels are numerous and of such a large size that the whole wall of the intestine appears in places like a large blood vessel. This condition is particularly evident in specimens that have been killed or hardened in chromic acid, a process which preserves the circular form of the blood corpuscles making the cell bodies transparent and the nuclei distinct. This highly vascular condition is not perhaps exaggerated in these young forms but the proportion between the size of the blood corpuscles and the animal seems to emphasize it.

All investigators agree that there are no multicellular glands present in the intestine of the larva or adult *Petromyzon Planeri*. There are no explicit statements as to the condition of the epithelium in the large larvae ; Langerhans (35) says the epithelium of the mid intestine has long been known to be covered with cilia. All general statements in zoological works are to the effect that the intestine is ciliated throughout its length. A definite reference is made by Scott (53), who says that the intestine of the embryo is ciliated all round but he does not say what the condition is in older forms.

The larvae of the lake lamprey give somewhat different results some of which might be anticipated and others are rather surprising. With the total absence of glands a differentiation of the surface epithelium cells for secretion and absorption is to be expected and this condition is found true. The alimentary canal is not ciliated throughout ; there are many areas of ciliated epithelial cells in the branchial cavity and the action of these cilia is very active and rapid. The cephalic part of the alimentary canal, the esophageal stomach, has at first four distinct folds (Fig. 6), that are plainly indicated by inward projections of the subepithelial tissue. The largest fold is dorsal and the others ventral and lateral. The distribution of ciliated cells is somewhat irregular but in general the free edges of the folds bear ciliated epithelium, while the grooves between them, which are deep and somewhat narrow, are lined with cells having a striated border (Fig. 6). In places smaller folds appear and these are sometimes ciliated on the elevations and sometimes striated. Cilia do not seem to be present in a continuous line even on the folds. Just cephalad of the beginning of the intestine there appear scattered among the cells with striated borders large granular cells that are non-ciliated and are rendered especially conspicuous by staining blue in hydrochloric acid carmine (Fig. 6). Two of the four folds gradually approach each other and toward the caudal end of this part of the enteron there are but three folds, one still maintaining a dorsal position.

Immediately on entering the intestine the structure is recognizably different. Visible to the unaided eye extending down the intestine opposite the spiral fold is a golden yellow line of varying width ; there are also on the free edge of the typhlosole interrupted lines and irregular areas of the same color (Fig. 7). When examined under the microscope the yellow color is found to be due to the contents of cells that are crowded with large and small yellow globules ; large masses of the same substance were found on the intestinal surface. There is no line of demarcation where these cells cease and others begin ; they gradually become fewer in number and the contained globules smaller. Nowhere on the surface of these cells can ciliary movement be seen though the animal was freshly killed and ether had not been used. At the cephalic end of the intestine there appear small areas on which cilia could be seen moving vigorously apparently projecting from the general surface.

Tissue containing the yellow material was put in osmic acid for twenty-four hours with the result of darkening but not decidedly blackening the globules. In a mass the colour was black but in single cells the contents showed a peculiar yellowish-green tint. The examination of a series of slides, some stained with hydrochloric carmine and some with hematoxylin and picric alcohol, showed uniformly a yellowish color on the epithelial border in these places. The size of the globules was very noticeable, in many cases they were as large as the nuclei and lay one behind the other in the same cell (Figs. 12, 13). These cells extend round a large part of the intestine, but never at the sharp turns occasioned by the projection of the typhlosole. At intervals there are peculiar interruptions in the continuity of the distribution of these cells. It is very evident that they are all non-ciliated ; isolation shows them to have a double border, an inner clear and an outer striated band (Fig. 13.) At irregular intervals among them are interspersed strange cell masses that project from the general cell surface in a fan-like wedge and are distinctly ciliated (Fig. 12). There is no regularity in the size and position of these groups but they extend for only a very short distance, one to two centimeters caudad of the liver. The remaining part of the epithelium is non-ciliated and bears a striated border.

To fully understand the function of these cells would require a careful series of physiological experiments. Only a few were tried which were extremely suggestive, almost conclusive in their results. A larva fourteen centimeters long that had been kept in running water for some time was put into a mixture of water and milk. It was left in this for six hours then etherized and examined. The position of the intestine could be seen through the body wall as a white line extending to the vent, indicating that the milk had traversed the whole length of the canal. On opening the body the position of the intestinal vein and typhlosole could be seen clearly outlined against the white contents of the intestine. The whole esophageal-stomach and five-tenths to one centimeter of the intestine were filled with a watery fluid in which floated particles of firmly coagulated milk ; the remainder of the intestine contained a solid mass of clotted milk. The yellow cells were exceedingly full of globules and masses of that substance could be found among the milk clots ; but as no effort was made to keep the clot from contact with the cut edges of the intestine, this is not conclusive evidence of their normal presence there. No globules were found in some substance that had been pressed from the intestine through the vent. The conditions appeared perfectly normal the only change being in the increased quantity of the yellow material present in the cells and outside among the intestinal contents.

The experiment was repeated with starch. A larva was put in a dish of water containing corn starch and left there for four hours ; at the end of that time it was killed with ether and examined. Practically the same results were obtained as before.

The starch filled the intestine excepting the cephalic part which contained some water. The yellow material was found in the same places but the amount outside the cells in the intestinal contents and on the surface of the epithelium was not as great as in the first case.

Another animal was put in about an eight per cent. mixture of water and milk (400 cc. of water, 30 cc. of milk); the water used was taken from a Pasteur filter. The animal was left in this mixture four hours ; it was not very active and when taken out seemed in a dying condition ; its reflexes were strong, indicating a high degree of vitality. The same peculiarities were found as in the foregoing cases, excepting that the yellow line of cells opposite the typhlosole was noticed as distinctly visible from the outside of the intestine and with the aid of a low power lense could be traced almost to the level of the end of the fold. The amount of globular material in the cells was not as great as in the first specimen fed, but was equal to that of the one fed on starch. The milk was clotted as before and in every way presented similar features. A third specimen taken from running water showed the same substance at the same places, but the amount of yellow material was noticeably less than in any of the fed specimens.

Parts of the intestine and of the liver of the larva fed four hours on eight per cent. milk, were put into one per cent. osmic acid for twelve hours then into a preparation of gum arabic for the same length of time and cut on the freezing microtome. The results were interesting and suggestive. The peculiar arrangement of ciliated cells was found to extend through only the first and second centimeters of the intestine. These groups occurred irregularly on both the typhlosole and the opposite surface but never at the angles of the intestine which were lined with extremely tall epithelium. The yellow granules were abundant and browned to a dark shade almost black. Besides being in the epithelial cells, granules were abundant in the muscular and cavernous layers of the alimentary canal. They vary much in size but are never as large as those contained in the cells ; they color in osmic acid and may be the same as the cellular material which in small particles closely resembled them. Some tissue containing the yellow cells from the starch fed specimen was also treated with osmic acid ; the cellular substance though very abundant was not affected in the least, not the slightest coloring could be detected. It is interesting to note that the series of sections showing the presence of so much yellow material in the intestinal cells and the strange blue-stained cells in the oesophageal-stomach was cut from a larva that had been kept in starch and water for about twenty-four hours, so that it must have been in the condition of active digestion.

These experiments suggest almost to a certainty that the cells with striated borders are absorbent in function. The contents varying in fatty nature according to the nature of the food. This view is certainly supported by the part believed to be performed by cells of this structure in the small intestine of frogs and mammals; careful experiments have shown that in these animals their function is largely fat absorption even if there is no other.

If the similar cells of the larval lamprey intestine are also absorptive in character they are evidently not restricted to fat absorption.

*Accessory Organs.*—The liver of the European larva has been very fully described in structure by Langerhans (35) and the larvae studied for this investigation show similar characters. The liver is a simple tubular gland with a large gall bladder buried on its right side at the cephalic end. There are numerous gall ducts through its substance leading to the bladder and one emptying into the intestine. All are lined with low cubical epithelium that appears as if ciliated at the entrance to the intestine but though some serial sections suggest this condition very strongly there has been no absolute proof of its truth. The general appearance of the liver tissue itself is of a solidly packed mass of cells arranged in tubules. Each little mass of tissue is composed of cells grouped around a small lumen (Fig. 22). The cells are irregular in shape and contain large nuclei situated at the base. Langerhans (35) says that the liver of the larval *Petromyzon Planeri* is distinguished from that of the adult by the almost, if not complete, absence of fat. This is not true in this form in specimens from thirteen to fifteen centimeters in length. On testing the liver with osmic acid there was found to be a large quantity of material stored in the liver cells which became undoubtedly black. This substance was present in the form of small and large globules usually placed in the outer part of the cells, the nuclei occupying the inner part (Fig. 22). No such substance was present in the cells of the bile ducts which under a high power show a rather coarsely granular structure of a yellowish color. The same colored material, though structureless, was present in the lumens of the ducts (Fig. 22). Fat was demonstrated in the liver of a larva taken from running water and also in one fed four hours on milk. In the latter case beside the usual quantity of fat a large amount of a different material was found to be present. There were many globules resembling those in the muscular wall of the intestine; the appearance was in many cases such as to suggest an intralobular position but this point is not decided.

*Pancreas.*—Regarding the presence of a pancreas in the adult or larval Petromyzon there has been much dispute. For a long time these animals were considered to possess no such organ but later investigations have modified this view by the discovery of a group of gland-like structures in the wall of the larval intestine and in the adult between the intestine and esophagus where the two overlap. Kuppfer (34) in his article on the embryology of *Petromyzon Planeri* gives a history of the different views held concerning these appendages in the larva. August Müller (39) first suggested that they might be a pancreas ; Langerhans thinks them a series of stomach glands ; Schneider (50) thinks they may be homologized with the spleen but assigns no definite reason beyond his failure to find any outlet into the intestine. Nestler (41) speaks of a structure present in the transforming larva that he considers the organ described by Langerhans enlarged. All of these investigators have really left the question much where they found it, their views being based upon conjectures. The most satisfactory knowledge comes from Kuppfer's (34) embryological work. He finds developed in the dorsal intestinal wall of the young three millimeter larva a diverticulum that he considers a pancreas. It clearly opens into the intestine and with the development of the animal spreads out latero-ventrally. Gradually the ventral opening from the liver to the intestine closes and by breaking through the tissues a connection is made to the right half of the dorsal pancreas ; the left half changes into lymphoid tissue. Owing to lack of material he carried the investigation no farther so the origin of the structure found in the larger larvae is still unknown. He says that he doubts whether the later structure can be considered a pancreas. A condition similar to that described for the European form was found (Fig. 24), but no further study was made of it. The results of this investigation upon the larval enteron may be briefly summed up as follows :

(1). The esophageal-stomach is traversed through its cephalic end by four longitudinal folds which are reduced to three in its caudal end. It is lined with tall columnar epithelial cells that are ciliated on the ridges and have striated borders in the grooves. There are at the caudal end specialized granular cells that stain differently from the rest in digestion.

(2). The intestinal epithelium is composed chiefly of cells with striated borders containing yellow globules and extending throughout the canal excepting in its extreme caudal part. There are also groups of ciliated cells projecting above the general surface and restricted to the cephalic end.

(3). The physiological experiments have demonstrated the presence of a fluid capable of coagulating milk, and that absorption takes place through the agency of the striated-bordered cells of the intestine.

(4). Fat is contained in the liver cells of larvae from thirteen to fifteen centimeters in length as demonstrated by treatment with osmic acid. There is also a substance present that is not affected by osmic acid.

## THE HISTOLOGY OF THE ADULT ENTERON.

The enteron of the adult is much changed from that of the larva. An esophagus has been developed and the intestine has become far more complex in form ; besides the spiral turns already mentioned, there are both in the esophagus and intestine, many long folds that project into the lumen of the canal, nearly filling it with thin sheets of mucosa. The folds run parallel to the typhlosole and are somewhat comparable to the valvulae conniventes of the human intestine. They are very variable in size and do not bear any constant proportion to the diameter of the canal. They are arranged with two long folds at some little distance from each other with shorter ones between them (Figs. 8, 9).

*Esophagus.*—(Fig. 15). The esophagus in general appearance closely resembles the intestine though much reduced in size. Some of the folds of mucosa are long, and shorter ones are interspersed between them, all having a somewhat spiral turn. In places the muscular walls are strongly developed showing two distinct layers. The epithelium is composed of low columnar cells that have neither ciliated nor striated borders ; the folds are composed of two layers of this epithelium placed upon a very slight base of connective tissue. The latter thickens in places and here may be seen blood corpuscles. The overlapping of the intestine and esophagus affords a good opportunity to see the difference between the tissues of the two. The general appearance of the intestinal epithelium is of less density, its cells are narrower and longer and seem to be less firmly connected with each other. The arrangement of the folds is similar, but where the typhlosole is developed the lumen of the canal is still more completely filled with mucosal laminae.

*Intestine.*—In the adult as in the larva there is but a single layer of epithelium without glands. If the tissue of the intestine just cauded of the liver is examined fresh its surface presents the appearance of being completely covered with vigorously moving cilia; interspersed into irregular groups at equally irregular intervals are large granular cells non-ciliated and often projecting above the general surface (Fig. 17); the granules are small, of a bright greenish color. Areas also, show the bright line indicative of cells having the striated border. The examination of tissues hardened in different ways shows that the epithelium of the folds is irregularly depressed into pits and that the elevations between these pits are usually ciliated (Fig. 16, C.) The pits are lined with cells possessing a striated border among which are placed some that are larger somewhat flask-shaped or club-like and filled with greenish granules (Fig. 17, A.). Ciliated cells are most numerous between one and three centimeters caudad of the points where the intestine becomes free from the liver. At the most cephalic end of the intestine the cells with the striated borders are most numerous there being only a few tufts of ciliated cells at intervals. Gradually the latter become more numerous till the appearance is that of a ciliated surface interrupted by pits lined with cells having a striated border (Fig. 18). These latter cells contain various sized granules (Fig. 17 B), that blacken or at least become dark brown in osmic acid. This same material is present in all the tissues underlying the epithelium. It can be traced down the central core of the mucosal fold into the muscular tissues (Fig. 18). Most of the granules appear free but in other cases they are arranged in irregularly spherical masses so as to suggest the possibility that they are contained in cells. Although many writers hold the opinion that absorption during digestion is one of the functions of the wandering cells so many recent investigators have expressed a disbelief founded on the results of their work that no decision can be made in this matter.

If, as their position indicates, these granules are particles resulting from food digestion, they must reach the blood vessels of the intestine, for so far as known there is, in this animal, no other carrying agent to take them to the tissues. Wherever these granules appear in the folds of mucosa they are always surrounded by blood corpuscles that are evidently in the capillaries leading down the fold of mucosa toward the intestinal wall. In all cases where the material had any appearance of being in a cell it was closely surrounded by blood corpuscles.

It may possibly be that the corpuscles, as it were, hold the material together giving it the massed appearance suggestive of its presence in cells. A careful search was made in all the small vessels of the intestinal wall to see if the presence of granules could be detected and though in some cases the relations strongly suggested that such might be the case, no undoubted evidence was found.

There is not much to be said concerning the third kind of cell, those similar to the beaker cells described by Langerhans (35) in *Petromyzon Planeri*. They are present only in the cephalic end of the intestine in any numbers though they may occasionally be found near the change in the spiral, but never caudad of that point. Isolation preparations show them as elongated club shaped cells (Fig. 17, A), with neither striated nor ciliated borders. The granules are very even in size and fine compared with those contained in cells with striated borders. Nothing definite can be stated regarding their function though it might be suggested that they are secretive. A series of experiments ought to be made to determine their condition during digestion and fasting.

The most noticeable change in tissue going toward the caudal part of the intestine is the increasing quantity of globular material present in the cells having striated borders ; the ciliated cells also contain this substance but never in such large masses. The groups of ciliated cells become smaller but at the same time more frequent ; at the caudal end they appear as small tufts among the other cells. The striated border does not maintain a constant depth, it is lower at the caudal end of the intestine, but cephalad of the change of direction of the spiral it is very high and as strongly suggests cilia as in the case of the larva (Figs. 13, 17 B). The quantity of yellow material is so large in the cells toward the caudal end of the intestine as to render it probable that the greenish color so characteristic of this part is due, at least in some measure, to this cause.

An experiment similar to that tried on the larvae was atempted on an adult lamprey. A specimen that had been kept in a pail for a long time, was slightly etherized and a mixture of one-third milk and two-thirds water was injected through the vent till the body was felt to be hard. The animal fully recovered from the ether and showed more vigor than before the injection. After six and one-half hours it was killed by pithing and examined. There was very little material in the intestine ; the first chamber seemed entirely empty though a microscopic examination showed milk globules adhering to the surface of the mucosa. The ciliary movement was very vigorous and many of the large granular cells were seen projecting from the surface.

A little cephalad of the change of direction in the spiral valve the green color became very distinct, some traces of milk appeared that were as firmly coagulated as in the larval intestine. Coagulated milk was present near the caudal end but in small quantities only and the greenish color of the intestine continued to be very marked. The cells with striated borders contained numerous large greenish-yellow globules ; there were a few large greenish spherules of a different nature seen among the intestinal contents. Parts of this intestine were put in osmic acid and the rest to harden in Erlich's fluid and picric alcohol. The osmic acid specimens are very instructive, especially that part from the caudal end which was cut in whole trans-sections. The contents of the cells had been blackened to all appearances nearly as dark as the milk globules on the intestinal surface (Fig. 18). The substance could be seen massed in the central part of the mucosal folds in a solid line ; on reaching the subepethelial layers the line spread out in both directions. Careful search was made to see if any black particles could be found in the blood vessels, though conditions again were found strongly suggesting it, the vessels were too small and the appearances too liable to deception to justify a decision.

All of the osmic acid preparations showed the same general features ; the position of the ciliated cells was indicated most clearly and though most of the yellow substance was contained in the cells with striated borders it was present also in the ciliated cells. Throughout the enteric epithelium there appear small, round cells at irregular intervals imbedded among the epithelial cells. Sometimes they are isolated and sometimes in groups of two or three.

Just what these cells are and what their presence signifies cannot be decided from the present data ; but from the work of Heidenhain, Schäfer and Stöhr there is good reason to think they are leucocytes. The investigations of Claypole (7) on *Necturus* and *Cryptobranchus* prove the presence of these wandering ceils in the epithelium of the digestive tracts of these animals. It is therefore not unreasonable to think that a similar condition may exist in *Petromyzon*.

*Changes during the Spawning Season.*—During the spawning season, which lasts from the end of May to the third week in June, the last changes known to take place in the enteric structure of the lake lamprey occur, and in some respects these are the most striking of the series of modifications to which the digestive tract is subjected. At a date presumably about two to three weeks preceding the time when the eggs are laid, a sudden increase in the size of the gonads of both sexes takes place, the increase being more marked in the female than in the male. At the same time the alimentary canal begins to atrophy and the liver changes color from orange to dark green. The reduction in the size of the intestine must take place with great rapidity, quite frequently the structure of the first lampreys ascending the streams in the spring have undergone but slight modifications. By the time the sexual products are matured the intestine is reduced from a tube of about one to one and one-half centimeters in diameter at the largest part to one measuring no more than two to three millimeters. (Figs. 9 and 10). In the body it appears as a fine thread hidden in the foliated, largely developed gonad. The characteristic appearance of the spiral coils and the reversal have almost completely disappeared, if there is any spiral twisting it is not for more than one or two turns. The canal is now no longer than the body cavity and is as straight, almost, as in the larva. Strange to say the reduction in size of the intestine takes place to an equal degree in both the males and females (15) though the gonad of the former is not so strikingly enlarged as that of the latter. Specimens were examined both before and after the discharge of the sexual products and contrary to expectations the reduction was slightly less in the latter stage.

Tissue was hardened in both cases in Fish's picro-aceto-sublimate (50 per cent. alcohol, 1,000 cc., glacial acetic acid, 5 cc. mercuric chloride, 5 grams, picric acid one gram.) and imbedded in paraffine. The intestine was in the condition shown in figures 10 and 19. The folds were much reduced in number and size but more in their length than in their breadth. The epithelium is low cubical and ciliated with no signs of the pit-like depressions or striated bordered cells. At the bases of the folds the process by which reduction takes place is seen. The epithelial surfaces come together and gradually fuse forming a syncytium the nuclei of which blend imperceptibly with those of the underlying tissues. The tissues are crowded with small fat-like globules that blacken or at least become dark brown in osmic acid. The lumen of the canal is very small and the general appearance closely resembles that of a brook lamprey at the same time of the year. One of the most prominent features is the large size of the portal vein which is filled with blood, (Fig. 10). The folds on the typhlosole have disappeared almost completely, leaving it with almost a plain epithelial surface. Tissue from specimens that had shed the sexual products showed no further reduction ; in some places the nuclei were smaller and appeared massed as if they might be forming a center of new growth. The esophagus also is reduced in diameter though not to the same degree as the intestine. The folds are irregular, some being much longer than others and in some places the epithelium, the cells of which are small and lower, suggests a ciliated surface. If this is true it is contrary to the evidence of fresh material. When examined fresh there was no sign of ciliary movement in the esophageal tissue though it was very evident in the intestine. The greatest change in the macroscopic appearance between these two stages is the nearly continuous, uniform pale green color of the intestine in the later stage. The dry cell battery was used and produced a slight contraction in the diameter of the tube after a continued stimulation. On the whole there is no appearance of dissolution of the tissues ; the change is purely one of reduction in the number of cells, those remaining preserve their functions and apparently are capable of all activities. From the condition of the intestinal tissue at the close of spawning season there is really no apparent reason why reconstruction could not take place.

*Liver.*—This organ in the lamprey has been the subject of much discussion and is a curious puzzle to physiologists. There is no gall bladder or bile ducts and no connection with the intestine. In structure the cells are small and grouped in lobules that vary considerably in size (Fig. 23); the cells are crowded with fat, the arrangement of which is irregular sometimes around a central nucleus and always completely filling the cells. In the place of the bile duct of the larva as was shown by Schneider (50) and Nestler (41) for *Petromyzon Planeri* there is a glandular structure composed of larger cells than the liver cells. The arrangement in lobules is similar and the general appearance is of a finer grained, more translucent substance (Fig. 28). There is apparently no connection with the intestine though the mass projects into the folds. This mass is first seen in a series going caudo-cephalad among the liver cells close to the entrance of the portal vein and near the hepatic artery. The cells besides being larger have larger nuclei than the liver cells and are always distinguishable by taking the stain differently. Two series were stained variously with hematoxylin, eosin, fuchsin, erythrosin, and picro-fuchsin-hematoxylin; in every case the stain distinctly differentiated the mass; in some cases it took a darker and in others a lighter shade. In one place the gland shows a structure suggestive of a partially closed duct which ends suddenly, reappearing to disappear again. The cells are in the caudal part arranged with a distinct lumen but no connection with any part of the intestine could be found. The nearest approach is made when some of these groups of cells lie directly beneath and in contact with the intestinal epithelium.

The liver of the specimen fed on milk as well as large quantities of fat showed a material that did not blacken with osmic acid. A piece of the tissue immediately after the death of the animal was treated with iodine and showed globules of the characteristic cherry-red of glycogen.

*Spleen* (?).—The history or rather ontogeny of this organ in the lampreys is still a mystery. That it acquires the form known in the adult during transformation is evident, but whether it is a modification of the isolated glands of the larva or a new growth is unsettled. The facts as they stand are, that between the intestine and esophagus where the two canals overlap is situated a gland-like mass in some places as large in diameter as the esophagus. Following the curves of the intestine and esophagus it is at its largest part dumb-bell shaped and later separates into two lobes. The structure of this body is somewhat complex. In places the cells seem simply grouped round a lumen regular in form and with the nuclei in the base (Fig. 29) ; in other cases the cells appear as if massed together without any particular arrangement and surrounded by connective tissue ; in the former case the cells are large and in the latter small. There are numerous blood vessels especially toward the caudal end of the structure and a large vessel is finally formed that uniting with intestinal veins empties into the portal vein. This organ is prolonged caudad in small groups of cells that lie in a fold of mucosa ; these are the parts that preserve most perfectly the open lumen. In one series extending through the cephalic part there are several peculiar large vessel-like structures that do not apparently contain any blood corpuscles, in one place there are two such opening into each other. In the esophageal epithelium at this point are several small openings of the same nature but the relations of these were not fully investigated.

There is one point in regard to this organ that is very interesting and worthy of future investigation. In all the blood vessels connected with it there are a great number of leucocytes ; in places where the structure is indistinct there are numerous small cells suggestive of the small white corpuscles found in the circulating blood (Fig. 29.) In the veins spoken of above the same proportion in the number of leucocytes holds, and this fact though a mere isolated observation suggests the idea that this organ may be of a lymphoid nature. An experiment might be tried by injecting carbon into the system and seeing whether any appeared in the cells of this organ. If this should happen, judging from the result with *Necturus* (7), there would be one more presumption in favor of Schneider's opinion as to the homology of this organ with the spleen.

The following is a brief summary of the results obtained from the investigations on the adult enteron :

(1) The mucosa of the esophagus and intestine possesses many long folds that project into the lumen of the canal.

(2) The esophageal epithelium is composed of undifferentiated low, columnar cells with neither ciliated not striated borders.

(3) The intestinal eipthelium is differentiated into ciliated cells on the plane surfaces or in tufts; cells with a striated border lining pits and spaces between the ciliated tufts; large club shaped granular cells scattered among the others and restricted to that part of the intestine cephalad of the change of direction in spiral fold.

(4) The physiological experiments show the presence of a ferment capable of coagulating milk and that the cells with striated borders are absorptive in nature. The folds of mucosa in their absorptive function resemble the villi in the small intestine of mammals.

(5) The liver contains large quantities of fat and also a substance giving the characteristic reaction of glycogen.

(6) There are present in the organ lying between the esophagus and intestine numbers of leucocytes suggesting a lymphoid character.

(7) The typhlosole makes from 4–6 turns beginning dorsally and ending ventrally; it shows a reversal of direction taking place at a point ⅔ of its length from the cephalic end.

## HISTOLOGY OF THE TRANSFORMING LARVAE.

Three distinct stages of transformation were studied. One specimen was in a very early stage when its mouth had not assumed an oval shape; the corners of the upper lip were still visible and the eyes were hardly more distinct than those of the true larva. It was put in a test tube with starch during life and showed inspiratory currents through the mouth and expiratory through the branchiopores. Its stage in development did not admit of the determination of its species. This particular specimen came from the Susquehanna but as no recognizable brook lamprey has been brought from the same place, the presumption in favor of its being a young *Petromyzon marinus* amounts almost to a certainty. A second specimen brought from Cayuga lake in December was to all external appearance ready for a parasitic life. It had the adult form of a head and mouth ; the peculiar sheeny, slate-grey color of the young parasite and freely attached itself to the jar during life. A third specimen was in the same condition externally when caught in December and remained buried in the sand throughout the winter emerging in March and refusing to return. On trial with starch and water a slight current was found to flow in through the mouth.

Larva I was brought in from Owego August 24th, and showed the above mentioned incomplete external changes. It was sixteen and five-tenths centimeters long and had not completely changed its coloration. It was killed in one-third per cent. chromic acid and left in this mixture for twelve hours ; it was then hardened in picric alcohol and cut by the paraffine method, several different stains being used. It was a female and the gonads contained distinctly developed ova.

The region of the liver showed most interesting features both as to the intestine and the liver itself. The former just caudad of the liver is very much contracted in size, the walls are collapsed and the opposed ental surfaces fastened together by a material staining dark blue with hematoxylin. The epithelium and underlying mucosa are raised into numerous low folds projecting into the lumen of the intestine ; these folds are evidently centers of growth as they are composed of many closely packed small cells. Going cephalad the tissue seems less in a state of histogenesis than in a state of histolysis. In the esophageal-stomach the epithelial tissue is in some places a mass of transparent substance that has taken no stain and shows no distinct cell outlines (Fig. 26). Under the least formed epithelium lie masses of small cells that are pushing forward, taking the place of the breaking down epithelial cells. The mesenteric vein is in this part large, distinct and functional, the latter is evidenced by its being full of blood and having a complete connection with the liver.

The liver is undergoing as great changes as the intestine. The cells are smaller than those of a larval liver and there is no evidence of a gall bladder ; throughout its tissue there appear at intervals bile ducts, but these change gradually into groups of liver cells. There is no duct opening into the intestine, the epithelium is continuous at that place. The duct can, however, be traced from just below the epithelium into the liver tissue. The walls are not made of cuboid epithelium as in the larva, but are formed of groups of cells arranged in follicles that even in small numbers of three or four stain differently from any of the surrounding tissue. The lumen surrounded by these cells contains a yellow substance resembling that seen in the larval bile ducts. Gradually this lumen is completely lost, a mass of cells remaining to indicate its past position (Figs. 24–28). Aside from the occasional traces of true bile duct tissue and the indication of where the duct communicated with the intestine, all resemblance to the larval liver is lost. This closely resembles the process described by Nestler (41) as taking place in *Petromyzon Planeri.*

Transforming larva II was thirteen and six-tenths centimeters long and as before stated showed the external characteristics indicative of complete transformation ; its eyes, mouth, and general shape resembling the adult. It was brought in from Cayuga lake in December 1893, and showed ability and willingness to attach itself to the vessel containing it. It was killed in one-fourth per cent. chromic acid hardened in picric alcohol and cut in transections by the paraffine method. The whole animal was sectioned from about one centimeter caudad of the vent. Gage's aqueous hematoxylin and Delafield's hematoxylin with picric alcohol and eosin as counter stains were used. This animal proved to be a male and showed but very slight development of the gonad.

The enteric tissue had changed throughout, it in no way resembled the larval conditions. There was no indication of any functional activity in the intestine, in fact the state of the lining tissue prohibited any such condition. The esophagus and caudal end of the canal were farthest advanced and appeared fairly complete in structure. The former showed inward projecting mucosal folds covered with rather low columnar epithelium that seemed perfectly formed. The caudal end of the intestine showed many incipient folds not fully formed, that evidently develop in two ways. One by the formation in the wall of the intestine of several layers of cells closely laid on each other (Fig. 20) ; these are gradually folded off as it were from each other, and in many cases can be seen still adhering by the surfaces of the epithelium which are not yet fully formed. The second way is by the excrescence of the subepithelial tissue which gradually pushing out the overlying epithelium increases to a full length fold (Fig.

21). There is nowhere any sign of ciliated surfaces or differentiated epithelial cells ; the latter are all low with very large nuclei. The intestine is greatly enlarged in diameter and its walls are extremely thin, being reduced in some places to the merest layer of tissue. In general the folds forming may be said to be localized in four to six centers (Fig. 11), one of which is the typhlosole. In these masses of growing cells the future mucosal folds are being developed, the walls intervening between these points being reduced to a minimum. In that part of the intestine which in the larva was the esophageal-stomach near the cephalic end of the liver there is really no definite structure. The tissue is apparently a homogeneous mass or syncytium closely filled with nuclei. There is no epithelium and the reduction in thickness of the walls in proportion to the increased diameter is at its greatest. The intestinal vein is present but at no part does it show functional activity ; both it and the artery are extremely variable in size, in some parts appearing distinct while again they will disappear and be almost absent. There are two distinct arterial branches coming from the aorta at the caudal end ; one, the inferior mesenteric that anastomoses with the intestinal artery, the other running out into capillaries. The former is surrounded by the mesenteric vein that connects directly with the right cardinal, the dorsal sinus not being formed. As can be seen from the foregoing descriptions the division found in the larval enteron have been lost. The esophageal-stomach is increased in diameter and is of equal size with the much enlarged intestine, with which it is continuous.

The liver is in structure very similar to that of the adult form, neither bile ducts nor gall bladder are present ; in the place of the former the large gland-like structure is fully developed and takes a characteristically different stain from the liver tissue, it is smaller-celled and does not extend into the typhlosole as in the adult but otherwise the relations are practically similar. The liver cells also are much smaller than those of the adult and present the general appearance of great growing activity, if this can be inferred from numerous cells of small size. Cephalad of this point between the opposed walls of intestine and esophagus is situated a structure similar to the one found in the adult. It is smaller in size and composed of more closely packed smaller cells but resembled it in shape.

Larva III was brought in under conditions similar to those of Larva II and resembles it closely in external appearances. On being put in water with sand it immediately buried itself and remained so until March, about three months, when it emerged and though left undisturbed for several days it refused to re-enter. It was killed in one-fourth per cent. chromic acid and hardened in successive strengths of alcohol. Sections show the tissues completely formed and with all appearances of fitness for functional activity; the epithelium is lower and more cubical than with the adult but in other respects is similar. This was a male and showed as in the case of Larva II but slight development of the gonad.

The observations on the transforming enteron may be summed up briefly as follows:

(1). An esophagus develops during metamorphosis dorsad of the bronchus.

(2). The intestine is at first collapsed but later enlarges greatly with a corresponding thinning of the walls. The distinction between the esophageal-stomach and intestine is lost, the former enlarges and becomes continuous with the latter.

(3). The tissues of the enteron undergo histolysis and histogenesis; the folds of mucosa arising during the latter stage.

(4). The bile ducts and gall bladder disappear and in the place of the former a gland-like structure arises.

(5). The intestinal vein is developed in the typhlosole; the inferior mesenteric artery is present and anastomoses with the intestinal artery as in the adult.

(6). The spiral turns of the typhlosole develop during metamorphosis.

## GENERAL SUMMARY.

The following are the results of this investigation:

(1). The larval intestine is simple, short and straight with no mucosal folds; there is a distinct division into two sections on the level of the entrance of the ductus choledochus, the smaller part cephalad and the larger caudad. The adult intestine is long and twisted spirally in two directions giving four to six complete turns. The mucosa is arranged in many longitudinal folds that project into the lumen of the canal. There is no demarcation into two parts in the region of the liver.

(2). In both larva and adult the intestinal epithelium is differentiated into cells with ciliated and striated borders. The former are restricted in the larva to the cephalic end of the canal; in the adult they are present throughout the whole length of the intestine. Striated cells are present in both forms in all parts excepting in the adult esophagus, and function in absorption. The mucosal folds of the adult act similarly to the villi of the small intestine in mammals.

(3). The enteric tissues of the larva undergo complete histolysis and histogenesis during metamorphosis.

(4). There is present in both adult and larval enterons a fluid capable of coagulating milk.

(5). Food passes with great rapidity through the larval alimentary canal and very slowly through that of the adult.

(6). Fat is present in the larval kidneys, is absorbed during metamorphosis and is present in large quantities in the adult liver.

(7). The time of metamorphosis is probably from the beginning of August to March. The transforming larva with the external appearances of the adult passes the winter in the sand emerging ready for a parasitic life in the spring.

(8). Size at metamorphosis is very variable and affords no clue to the approach of the change; specimens vary from thirteen and six-tenths to sixteen and five-tenths centimeters in length.

(9). The typhlosole increases from one-half a turn in the larval to six in the adult, in the latter case having a reversal of direction.

(10). The enteric tissue at spawning season undergoes great reduction, but at the end shows no sign that complete reconstruction is impossible.

A comparative study of the larval and adult intestines indicates fewer fundamental differences than seems at first sight possible. Cellular structures are similar only somewhat modified. The developments of the folds and twists found in the adult constitutes the most obvious difference. These possibly serve for several purposes; the former to increase the area of mucosa exposed to the contents of the intestine, the latter to retard the swiftness with which substance passes through the canal as well as for the accommodation of its length. Judging from the length of time these animals may be kept after taking them from their hosts and yet have food in the intestine, the rate of passage must be extremely slow. It is on the contrary very rapid in the larva as evidenced by the experiments made with starch. The enlargement in the size of the canal and the development of mucosal folds in the adult lake lamprey is markedly different from the condition found in the brook lamprey where the folds are mere raised points of mucosa and the diameter of the enteron is much decreased. It seems highly probable that this difference is due to the much longer life of the lake lamprey thus requiring greater specialization for its change in food. It is thought to be two or three years after transformation before the lake lamprey becomes sexually mature while the brook lamprey probably spawns in the spring following its metamorphosis (15).

The absence in the adult of any biliary system must be taken as an indication that its food does not require the presence of that fluid during its assimilation ; a series of physiological experiments on blood digested with and without bile or pancreatic fluid would probably throw some light on the question. It seems rather an inexplicable fact in animal economy to possess a large, well developed liver and yet have none of the fluid usually considered a part of it. As has been shown this organ acts in its capacity as a producer of glycogen and also contains large quantities of fat. This animal with no bile and no undisputed pancreas offers a promising field for physiological investigations on digestion. The experiments already performed show the presence of a milk curdling ferment. With such simple structural details the results of any experiments must be interesting.

There are many different views as to the length of time required for the transformation of the larva to the adult. Observations made on *Petromyzon Planeri* demand a time varying from a few weeks to five months. Schneider (50) says he finds no preparation for transformation, and concludes that it takes place very rapidly. However, it may be with the European brook lamprey it is certainly a period of considerable length in the life of the lake lamprey. External signs of metamorphosis may be seen in August and the process is outwardly complete by December. But when the first external signs appear there have already been profound internal changes and, as shown by the specimen kept alive during the winter, the ental reconstruction is not complete till the following March. At the inside estimate it requires seven months to completely transform the larva of the lake lamprey to an animal ready for a parasitic life. Upon what does it live during this period? It apparently takes nothing into its intestine and even if it should, it seems difficult to understand how it could assimulate it. As well known, the larval kidneys are filled with fat and some amount of the same substance is present in the liver; during metamorphosis the fat from the kidneys is absorbed and the dorsal sinus formed. Examination of a transforming liver gave no blackening with osmic acid, and though not a fresh specimen it had been treated as other tissue giving the reaction. Perhaps these two organs are used for store houses for food during the period of histolysis and histogenesis, a period in many respects suggesting the life history of some members of the group invertebrata. This suggestion is more forcible, yet if we consider the sexually mature period of the animal's life. What becomes of the lake lamprey after spawning? Are all the years of larval and immature life concentrated on the production of one brood of young? It seems probable that this is the case. The atrophy of the alimentary canal during the spawning season leaves the animal without apparent means of nourishment, and according to a recent writer (15) it probably lives but a short time after spawning. This is comparable with the insect imago living long enough to provide for the perpetuation of its species and then dying.

The transition between the vertebrates and invertebrates is one upon which the student of biology always ponders with a certain amount of curiosity and a longing to see how the very evident chasm can be bridged. Naturally his thoughts turn to the lowest vertebrates for suggestions and round the *Marsipobranchii* as well as *Branchiostoma* has centered the interest of many scientific philosophers; but so far little satisfaction has been obtained. The step between the highest invertebrate and the lowest vertebrate is too long, nor is it here that the strongest hint of resemblance should be sought. It is far back before either the invertebrate or vertebrate, as we now know them had existed, that the departure of the two branches from a common ancester took place. All that can be hoped is to find a few or perhaps one feature that may be considered characteristic of the generalized vertebrate.

Though ranked among the lowest of the vertebrate kingdom, *Petromyzon* is not primitive in structure. It belongs to the only class among vertebrates in which parasitism occurs, and arguing from the usual effect of this mode of life a degradation or simplification of structure is to be expected. This result is, however, not found, and not only does the complexity of the structure increase but in many respects the results are contrary to general rules. The larva, an animal taking its food from the water and swallowing a great quantity of sand and other waste material has a short and straight intestine through which material passes with great rapidity. On changing its nutrition to the most condensed form of carniverous food, its intestine elongates, becomes twisted and developes folds causing food to move very slowly. Its mouth is very highly adapted to its life as a parasite but it is perhaps equally essential for nest building during the breeding season. In respect to the complete absence of mesentery this animal stands almost alone; Owen (42) says that in some of the Syngnathi and Cyprinidæ a partial reduction has taken place, but it is evidently not complete. Not only is the mesentery absent in the larva and adult but in *Petromyzon Planeri* it is never present even in the earliest embryological life. Gœtte (21) shows that the two splanchnic layers meet and fuse immediately, separating the intestinal from the peritoneal serosa. The presence of mesentery in the adult would render such a twisting as takes place mechanically impossible. There is another fact concerning the adult animal which is surprising. The larva has strong vitality and can endure a considerable deprivation of fresh water, but the adult is extraordinarily susceptible to any such lack. Unless kept in abundance of running water it invariably dies in a few hours.

There is no doubt that the lamprey is low in the scale of vertebrates, recent palæontological discoveries (55, 56) indicate that it is an old form of life and its present lack of bony skeleton is a secondary development. Beard (3) considers its numerous, small, holoblastic eggs a primitive character, but that the lampreys are generalized vertebrates it is impossible to maintain. It was perhaps early in the history of vertebrates that the lampreys separated from the main branch and their upward course may not have been very great, yet their lateral divergence shows so much nicely adjusted specialization that they must be considered good examples of forms that unite with simple structure modifications showing great adaptability to the needs of life.

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## PLATE I. (Omitted.)

*Photographs of Adult and Larval Lampreys.*

Fig. 1. Lateral aspect of adult lake lamprey; length, 38.8 centimeters. Taken April 14th, 1894, and photographed fresh under water.

Fig. 2. Lateral aspect of larval lamprey, natural size. Preserved in alcohol and photographed under water.

## PLATE II. (Omitted.)

Fig. 3. Lateral view of intestine of adult lake lamprey; 38.7 centimeters in length. Taken in March. Arterial injection through the dorsal aorta with red gelatine mass. Photographed fresh under water.

1. Caudal point of the liver.
*a*. Change in direction of the spiral turns.
*b*. Intestinal vein.
*c*. Vent.

This specimen shows five complete turns, three cephalad and two caudad of the change in direction of the spiral. The change is dorsal thus making six complete turns. The loop formed by the intestine is natural and shows its length to be greater than that of the body cavity.

Fig. 4. Caudal part of adult intestine showing four vascular bands. A transection of the second is given in Fig. 5, showing the arrangement of the vessels.

*a*. Inferior mesenteric artery.
*b*. Intestinal vein divided into two by the artery.

Fig. 5. Diagram of the largest dorsal band showing the arrangement of the vessels.

| | |
|---|---|
| *a.* | Inferior mesenteric artery. |
| *b.* | Intestinal vein divided into two by the artery. |
| *c.* | Layer of tissue binding the three vessels together. |

## PLATE III.

### *Transections of Larval and Adult Enterons.*

Fig. 6. Transection of larval esophageal-stomach (× about 100).

| | |
|---|---|
| *m.* | Muscularis. |
| *m.c.* | Mucosa. |
| *e.* | Epithelium. |
| *g.* | Granular cells stained blue. |
| *x-x.* | Ciliated areas. |

Fig. 7. Transection of larval intestine just caudad of the liver (× about 45). This section is cephalad of the union between the cephalic branch and the portal vein ; this explains the slight vascularity of its walls.

| | |
|---|---|
| *T.* | Opposite typhlosole. |
| *L.* | Lumen of intestine. |
| *A.* | Intestinal artery in the typhlosole. |
| *P. V.* | Portal vein lying free outside the intestine. (Compare with Fig. 9,) |
| *H.* | Cavernous tissue of the typhlosole. |
| *m.m.* | Muscularis and mucosa. |
| *e.* | Epithelium. |
| *x-x.* | Average extent of yellow lines and areas. |

Fig. 8. Transection of adult esophagus (× about 20).

| | |
|---|---|
| *mf.* | Mucosal folds. |
| *mm.* | Muscularis and mucosa. |
| *e.* | Epithelium. |
| *mc.* | Mucosa. |
| *v.* | Vessel in the mucosa. |

## PLATE IV.

### *Transections of Adult and Transforming Larval Intestines.*

Fig. 9. Transection of the intestine of an adult 37.6 centimeters in length, taken in January, cephalad of the change in direction of the spiral. (× about 14.)

| | |
|---|---|
| *T.* | Opposite typhlosole. |
| *L.* | Lumen of intestine. |
| *A.* | Intestinal artery in the typhlosole. |
| *PV.* | Portal vein in the typhlosole. (See Fig. 7.) |
| *mf.* | Mucosal folds on the intestinal walls. |
| *mf.* | Mucosal folds on the typhlosole. |
| *mm.* | Muscularis and mucosa. |
| *e.* | Epithelium. |
| *mc.* | Mucosa. |

Fig. 10. Transection of the intestine of an adult lake lamprey about 38 centimeters in length, taken in the middle of May. This section is from the same region as that shown in Fig. 9. (× 45.)

| | |
|---|---|
| *T.* | Opposite typhlosole. |
| *L.* | Lumen of intestine. |
| *A.* | Intestinal artery. |
| *PV.* | Portal vein. |
| *mm.* | Muscularis and mucosa. |
| *p.* | Peritoneum. |

Fig. 10. *A*. The section figured in figure 10 drawn on the same scale as Fig. 9. (× about 14.)
*L.* Lumen of the intestine.
*PV.* Portal vein.

Fig. 11. Transection of larval intestine during metamorphosis. Length of larva 13.6 centimeters. Section from near the caudal end. (× about 36.)
*T.* Opposite typhlosole.
*L.* Lumen of intestine.
*A.* Intestinal artery.
*PV.* Portal vein. (Compare with Figs. 9 and 7.)
*mf.* Developing mucosal folds.
*mm.* Muscularis and mucosa.

## PLATE V.

### *Structural Details of the Larval Intestine.*

Fig. 12. Section of part of the larval intestine just caudad of the liver. (× about 700.)
*m.* Muscularis.
*mc.* Mucosa.
*e.* Epithelium.
*d.* Striated border of epithelium.
*C.* Wedge-shaped ciliated areas. (Compare with Fig. 16, *C.*)

Fig. 13. Epithelial cells with the striated border. (× about 1200.)
*d.* Striated border.
*c.* Clear band.
*p.* Food particles.

Fig. 14. Muscularis showing two layers at approximately right angles. (× about 300.)

Fig. 14, *A*. Isolated muscle cells showing their fusiform shape and irregular size. (× about 1200.)

## PLATE VI.

### *Details of Structure in the Adult Intestine.*

Fig. 15. Tissue of esophagus. The tip of a mucosal fold. (× about 700.)
*mc.* Mucosa.
*e.* Epithelium.
*v.* Vessel in the mucosa.

Fig. 16. Tissue of intestine of adult from the cephalic end. The tip of a mucosal fold. (× about 360.)
*mc.* Mucosa.
*e.* Epithelium.
*d.* Striated border of epithelium.
*C.* Ciliated areas. (Compare with Fig. 12, *C.*)
*g.* Granular cells.

Fig. 17. Surface view of epithelium. (× about 360.)
*g.* Granular cells. (See Fig. 17, *A.*)
*f.* Absorbent cells containing food particles. (See Fig. 17, *B.*)

Fig. 17, *A*. Granular cells that project beyond the general surface. (× about 1200.)

Fig. 17, *B*. Absorbent cells. (× about 1200.)
*d.* Striated border.
*c.* Clear border.
*p.* Food particles.

Fig. 18. Tissue of the caudal end of the intestine, showing the mucosal folds during active absorption. (× about 100.) Osmic acid hardened.

| | |
|---|---|
| *mm.* | Muscularis and mucosa. |
| *e.* | Epithelium. |
| *mc.* | Mucosa. |
| *p.* | Blackened food particles present in the epithelial cells, mucosa and intestinal wall. |

## PLATE VII.

### *Tissues of Adult and Transforming Intestines.*

Fig. 19. Tissue of the adult intestine during the early spawning season, May. (See Fig. 10.) (× about 360.)

| | |
|---|---|
| *mf.* | Mucosal folds. |
| *e.* | Epithelium. (Ciliated.) |
| *mc.* | Mucosa. |
| *ca.* | Capillaries containing blood corpuscles in the mucosa. |
| *b.* | Base of a fold in which nuclei are abundant, but cell outlines are lost as if these cells had fused to form a syncytium. |

Fig. 20. Tissue of larval intestine during metamorphosis. From the caudal end of larva II. (× about 360.)

| | |
|---|---|
| *mf.* | Mucosal fold developing by delamination. (See Fig. 21.) |
| *mm.* | Muscularis and mucosa. |
| *mc.* | Mucosa. |
| *e.* | Epithelium. |
| *k.* | Mucous secretion. |

Fig. 21. Mucosal fold of transforming intestine developing by excrescence. (× about 360.)

| | |
|---|---|
| *mm.* | Muscularis and mucosa. |
| *e.* | Epithelium. |

## PLATE VIII.

### *Liver tissue of Adult and Larva.*

Fig. 22. Larval liver tissue. (× about 1200.)

| | |
|---|---|
| *Bd.* | Bile duct. |
| *e.* | Epithelium of bile duct. |
| *h.* | Hepatic tubules. One left unshaded to show the fat. |
| *hc.* | Hepatic cells containing the fat. |

Fig. 23. Adult liver during the winter season. (× about 1200.)

| | |
|---|---|
| *h.* | Hepatic lobules. |
| *cn.* | Inter-lobular connective tissue. |
| *d.* | Inter-lobular granules which do not blacken in osmic acid. |
| *ca.* | Capillary containing blood corpuscles. |

## PLATE IX.

### *Transformation of the bile duct of the larva during metamorphosis.*

Fig. 24. Section through the region of the ductus choledochus in the early transformation stage shown by larva I. (× about 100.)

| | |
|---|---|
| *L.* | Lumen of intestine which is slightly collapsed. |
| *A.* | Intestinal artery in the connective tissue formed between the liver and intestine. |

*Bd.* Bile duct surrounded by follicles with no opening into the intestine.
*f.* Follicles in the intestinal wall.
*e.* Epithelium of the intestine.
*mm.* Mucosa and muscularis.
*cn.* Newly formed connective tissue.

Fig. 25. Section farther cephalad and through the region indicated by the brace in figure 24. (× about 100.)
*e.* Epithelium of the intestine losing its definite structure and becoming a syncytium.
*Bd.* Bile duct closing up to a mass of follicles.

Fig. 26. Section cephalad of Figure 25 through the same region. (× about 100.)
*e.* Epithelium of the intestine reduced to a syncytium.
*cn.* Connective tissue.
*Bd.* Bile duct surrounded by follicles and filled with a yellowish material. (See Fig. 22.)

Fig. 27. Section cephalad of Figure 26. (× about 100.)
*e.* Epithelium, a thin syncytium.
*Bdg.* Mass of follicles forming the bile-duct gland. Lumen of ductus choledochus is lost.
*A.* Artery.
*PV.* Portal vein approaching the liver.
*l.* Liver tissue.
*Bd.* Traces of bile ducts in the liver tissue.
*v.* Blood vessels.
*ps.* Peritoneal space between the liver and intestine.

## PLATE X.

### *Adult Glands, the Nature and Function of Which are not Understood.*

Fig. 28. Adult bile duct gland showing the tubular structure with small lumens.
*gc.* Gland cells with large nuclei indistinct outlines and fine homogeneous structure.
*cn.* Connective tissue.

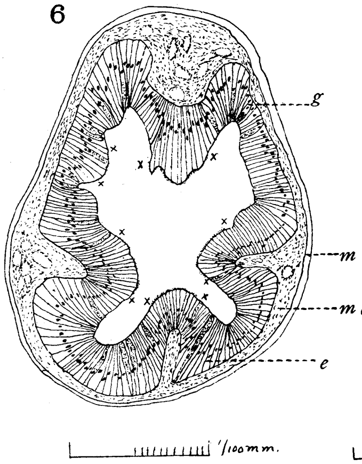
Fig. 29. Gland from between the opposed walls of the adult esophagus and intestine. (× about 120.)

Called by some the spleen and by others the pancreas. It shows irregular structure, the cells in some cases grouped so as to form a lumen and in others not.

*lc.* Leucocytes within an irregular lumen and also in an intralobular vessel.
*cn.* Connective tissue.

Fig. 29, *A.* Cells grouped showing a distinct lumen.

6



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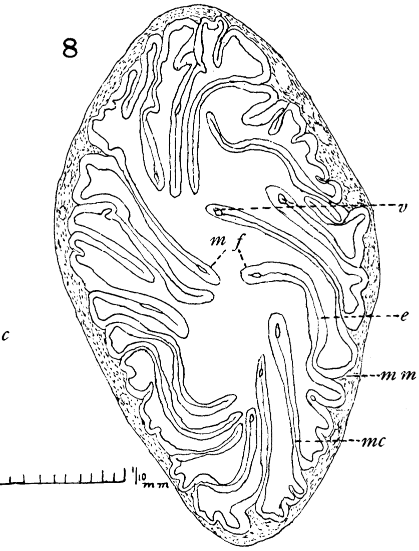

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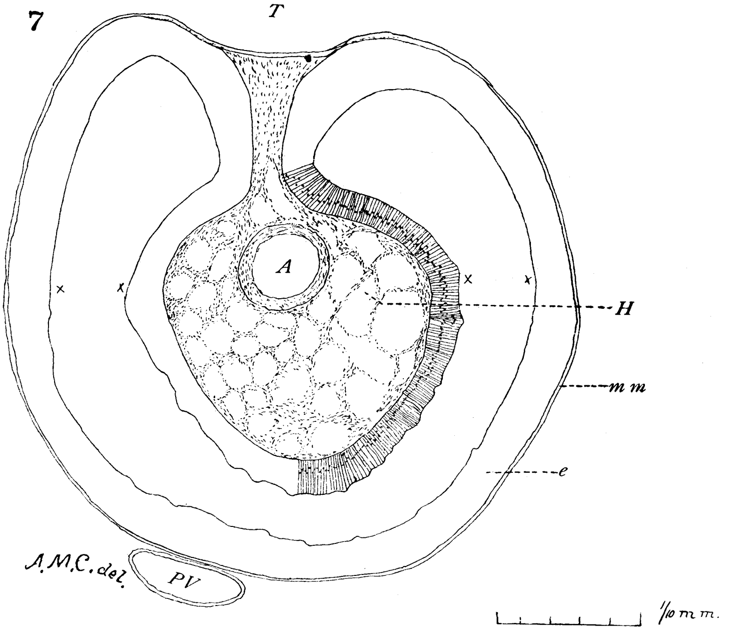
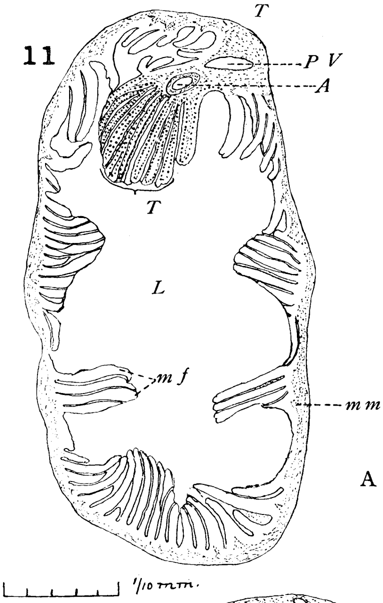


PLATE IV.

**11**



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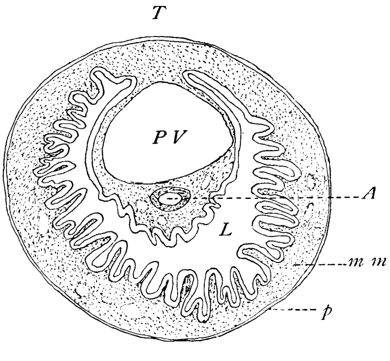
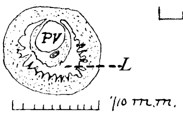


**A**



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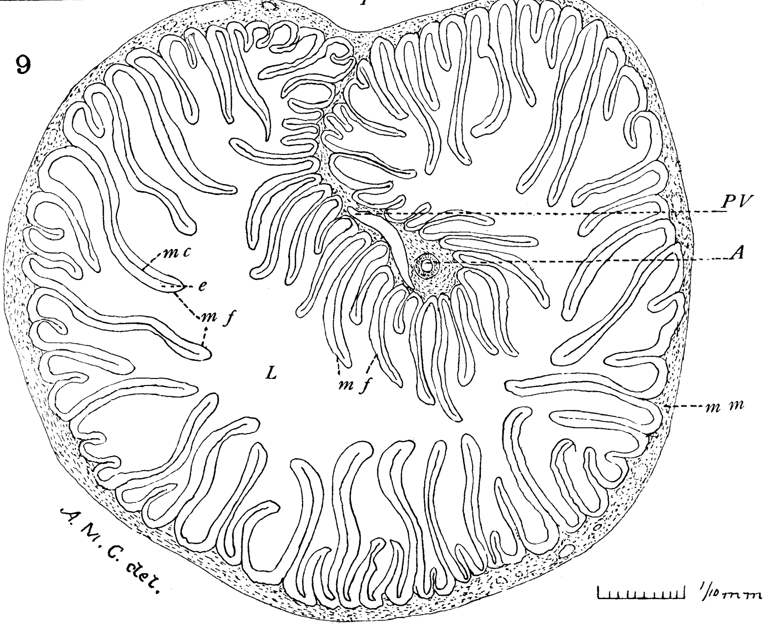
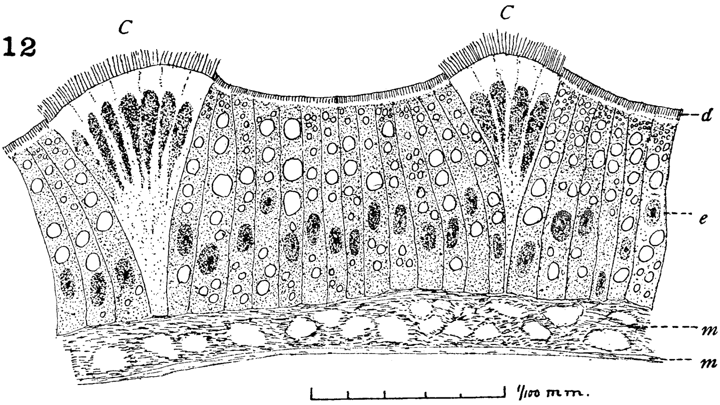


PLATE V.

**12**



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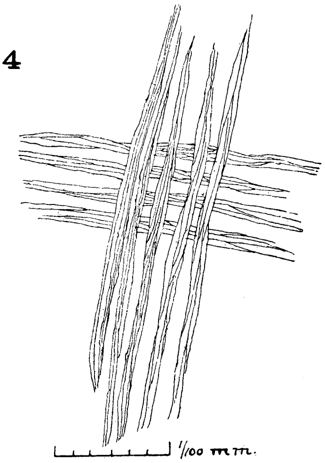

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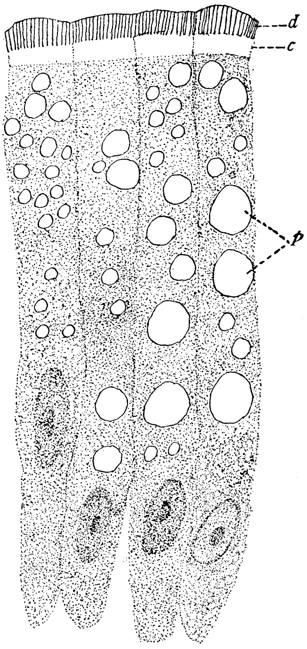

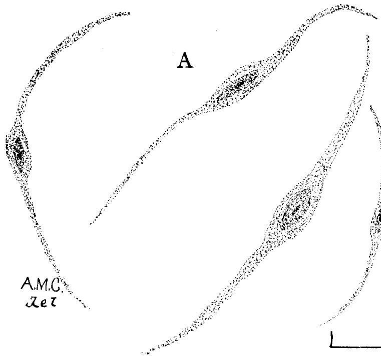

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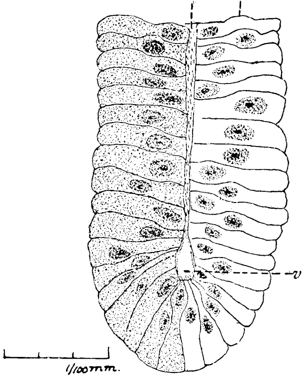
15



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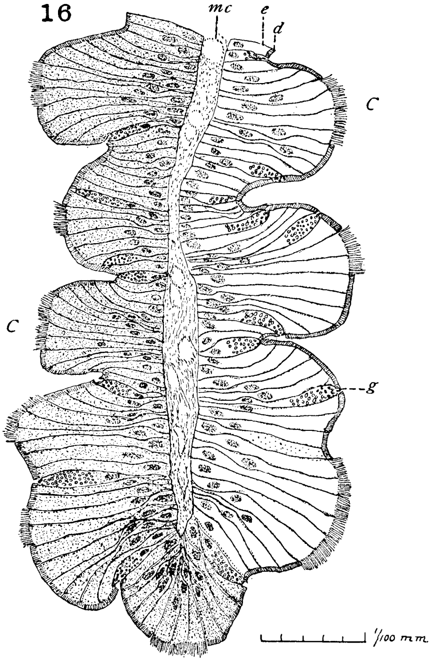

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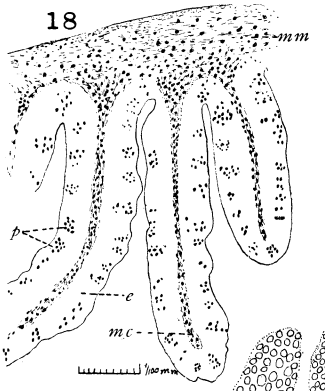

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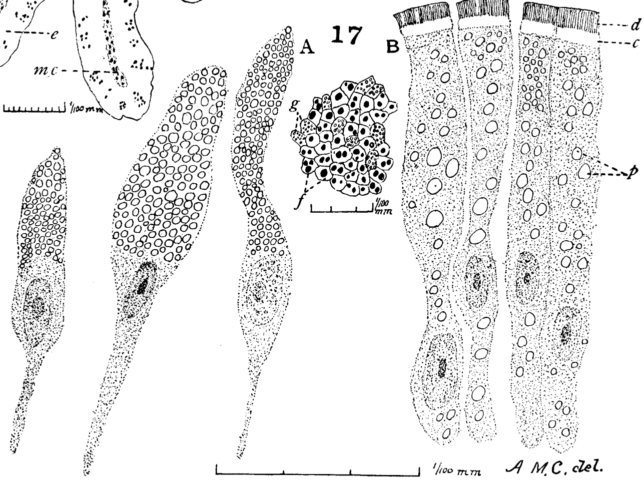
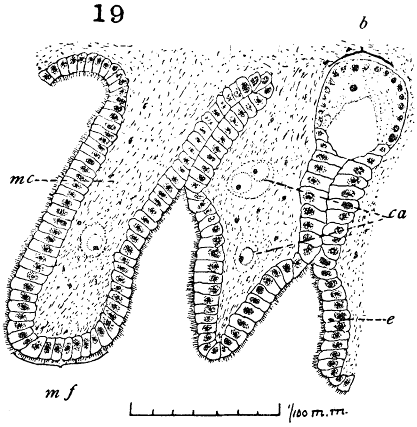


PLATE VII.

19



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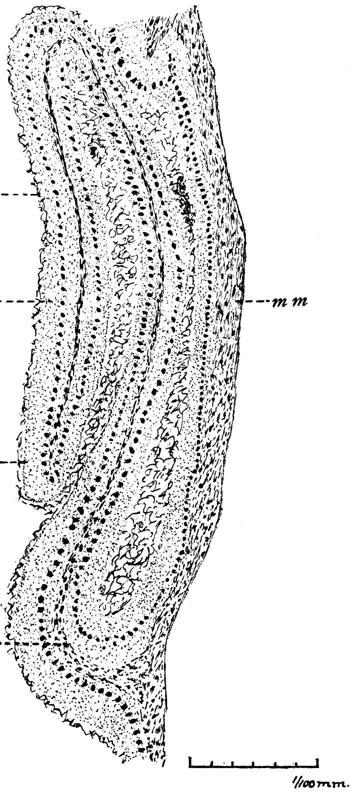

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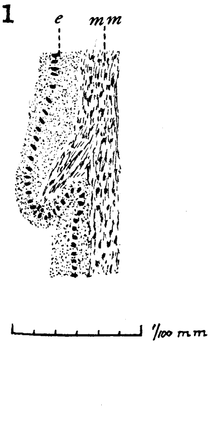
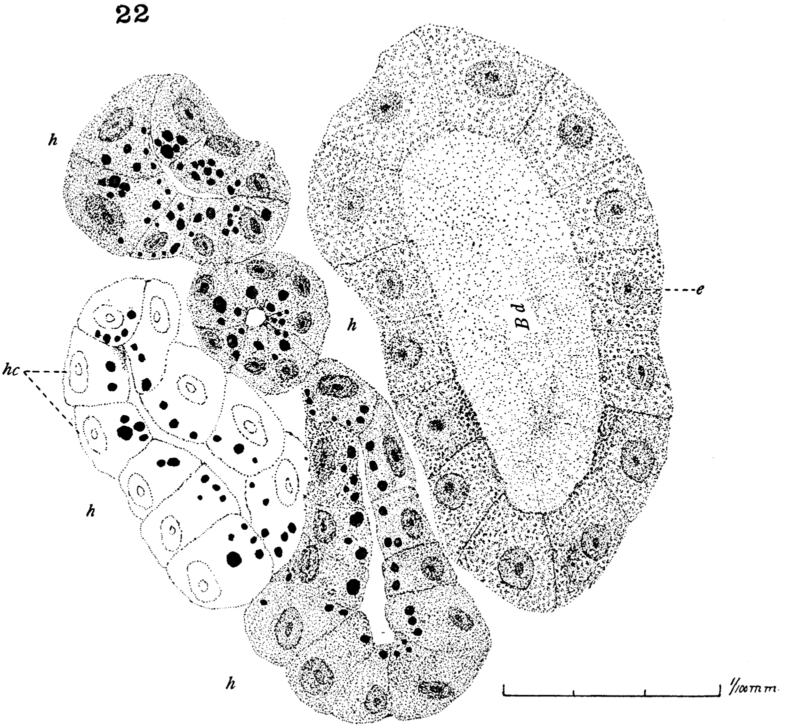


A. M. C. del.

PLATE VIII.

22



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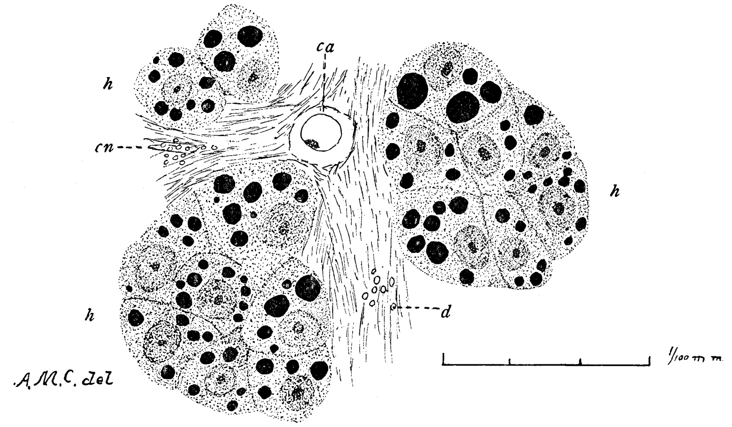
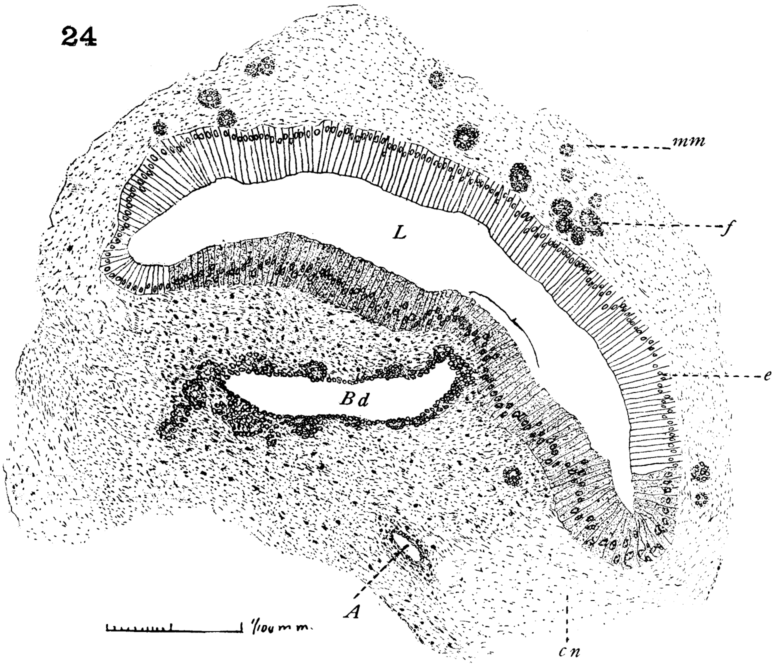


PLATE IX.

**24**



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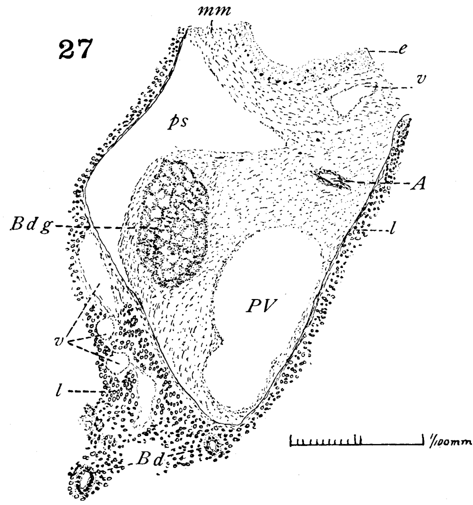

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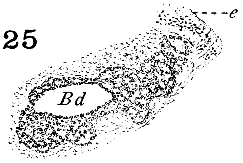

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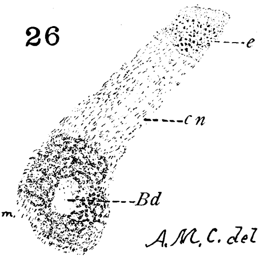
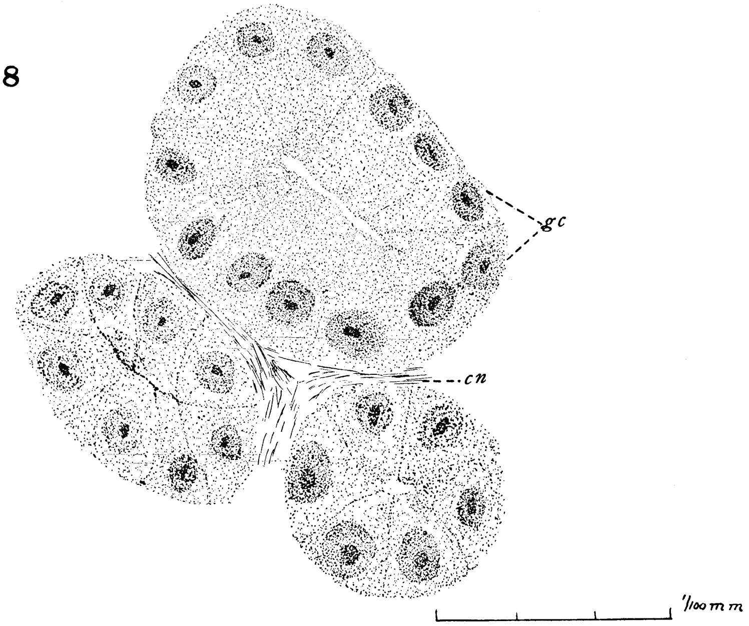


A.M.C. del

PLATE X.

28



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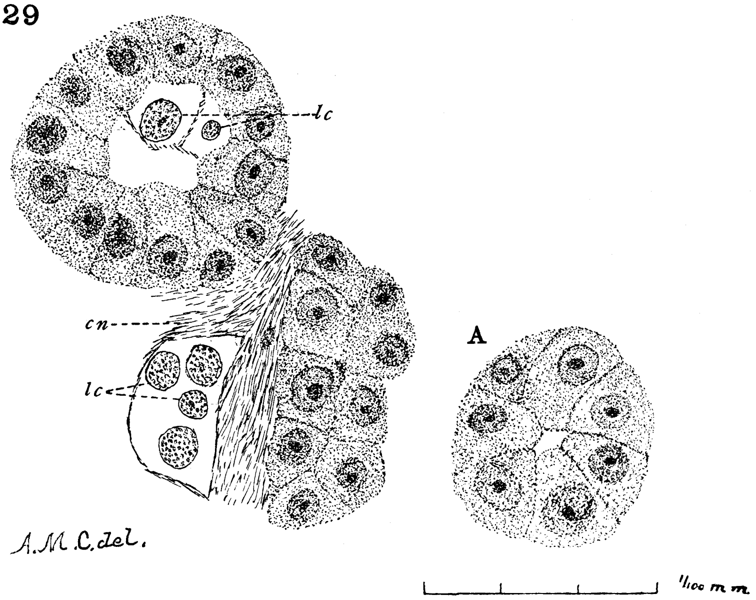

A.M.C. del.